Research Article

Connectivity and climate change drive the global distribution of highly invasive termites

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Abstract

Termites are amongst the most abundant and ecologically-important groups of insects in tropical forests. However, the destructive potential of some species amounts to billions of dollars in damage each year. Despite their economic and ecological impacts, only a limited number of invasive termite species have been studied using distribution modelling and no studies have taken trade, transport and demography variables into account. We used Species Distribution Models (SDMs) to investigate the potential distribution of 10 highly-invasive termites. Our study includes bioclimatic conditions, land-use patterns, elevation and connectivity predictors (i.e. urban areas, human population, accessibility to cities and private vessels), alongside different climatic and socioeconomic change scenarios.

The distribution of the termite species hinges on bioclimatic and connectivity variables, highlighting the significance of these latter factors in invasive species analyses. Our models demonstrate the potential of these invasive termites to thrive in large urbanised and connected areas within tropical and subtropical regions and to a lesser extent within temperate regions. As climate changes and urbanisation intensifies, most species' range could expand, particularly under a "fossil fuel-driven development" scenario. Furthermore, while some species may have a slightly reduced range, they could extend their presence into more urbanised and connected areas, increasing the risks and costs associated with termite damages. Our models highlight the anticipated role of growing connectivity and climate change dynamics in facilitating the widespread proliferation of invasive termites in the coming years.

Key words: Biological invasions, climate change, connectivity, invasive species, invasive termites, species distribution models

Introduction

Invasive species pose a significant threat to not only biodiversity by causing species extinction, but also mankind by spreading vector-borne diseases as well as imposing economic burdens to control invasive species (Seebens et al. 2018; IPBES 2019). Estimating economic costs of invasive species is a challenging task, requiring international and interdisciplinary expertise (Diagne et al. 2020), but recent papers suggest that the total reported costs exceed US$1.5 trillion (Angulo et al. 2021; Diagne et al. 2021). Such costs encompass lost product and service values, diminished crop yields, infrastructure damage, altered ecosystem services, medical expenses and costs related to invasive species control (Bradshaw et al. 2016; Hoffmann and Broadhurst 2016; Diagne et al. 2021). Alarmingly, the

overall cost of biological invasions – likely underestimated – triples every decade (Diagne et al. 2021).

The number of biological invasions is continuously rising, affecting even the most remote regions of the world (Seebens et al. 2017). In the coming decades, three main drivers – climate change, trade and transport and socioeconomic activities – will further impact biodiversity through biological invasions (Essl et al. 2020). Climate change, characterised by temperature increases, disrupted precipitation patterns and intensified extreme events (Seneviratne et al. 2021), will reshape the distribution of invasive species: some species will experience range expansions or contractions and previously unsuitable environments will become favourable for their establishment (Bellard et al. 2018). Shifts in trade dynamics, such as changes in volume and trade routes, will increase the number and sources of potential new introductions of alien species (Westphal et al. 2008; Humair et al. 2015; Eguíluz et al. 2016; Cope et al. 2019; Sardain et al. 2019; Essl et al. 2020). Despite efforts to strengthen quarantines and controls, alien species closely mirror trends in international trade, steadily growing (Liebhold et al. 2017; Hulme 2021). Moreover, ongoing land-use changes and socioeconomic development, particularly rapid urbanisation, will accelerate the establishment and spread of invasive species. Urban areas, serving as hubs for global material, food and energy flows (Decker et al. 2000), provide ideal entry and expansion points for opportunistic and invasive species (Bellard et al. 2016). Urban areas have already doubled since 1992 (IPBES 2019) and it is projected that up to 60% of the global population will reside in cities by 2030 (UN DESA 2020). This growing urbanisation results in significant biodiversity loss through the conversion of natural habitats to urban land (McDonald et al. 2020) and may create favourable conditions for invasive species.

Of the 3106 described termite species worldwide, 183 are considered pests and 28 are invasive (Oloo et al. 1990; Evans et al. 2013; Krishna et al. 2013). Termites are one of the most abundant and ecologically important groups of insects in tropical forests and play a crucial role as decomposers and ecosystem engineers, feeding on organic matter, including dead wood, leaves and roots (Holt and Lepage 2000; Eggleton and Tayasu 2001; Freymann et al. 2008; Jouquet et al. 2016). Termite pests, however, cause an economic impact of over US$40 billion annually worldwide (Rust and Su 2012; Evans et al. 2013; Krishna et al. 2013). Invasive termites cause extensive economic damage by infesting and feeding on various structures, including buildings, wooden furniture, utility poles and agricultural crops (Krishna et al. 2013). Consequently, preventative measures, such as quarantine regulations, early detection systems and integrated management strategies are crucial to prevent the introduction of invasive termites and minimise their spread (Rust and Su 2012; Evans et al. 2013).

Species distribution models (SDMs) can be a useful tool in preventing invasive species by identifying areas at risk of invasion and providing insights into their potential distribution in response to climate change and land-use modifications. While previous studies primarily considered bioclimatic factors to project distribution of invasive termites (e.g. Li et al. (2013); Buczkowski and Bertelsmeier (2017)), these variables oversimplify the complex trajectories associated with their spread in an increasingly interconnected and urbanised world (Essl et al. 2020). To address this limitation, we combined bioclimatic, land-use and elevation data with connectivity variables into SDMs. Connectivity variables are linked to trade, transport and demography and reflect the contemporary modes of termite dispersal. Historically, invasive termites were introduced through cargo and wood ship-

ments (Gay 1969), but strict quarantine inspections now mitigate new invasions (Scheffrahn 2023). However, private vessels like yachts or sailing boats, exempt from strict quarantine inspection, often traverse long distances through regions rich with termite species, posing a significant risk as potential vectors for termite invasions (Scheffrahn and Crowe 2011; Hochmair et al. 2023; Scheffrahn 2023). To our knowledge, our research is the first to consider connectivity variables (i.e. urban areas, human population, accessibility to cities and private vessels) into the framework of termite species distribution modelling. Their use is imposed by the decisive influence of human trade and transport in the spread of termites and by the presence of termites in urban environment and man-made structures (Gay 1969; Evans 2010). Our approach affords insights into the current and future distribution of ten highly-invasive termite species under two potential scenarios of Shared Socioeconomic Pathways (SSP2-4.5 "middle of the road scenario" and SSP5-8.5 "fossil-fuelled scenario") for two future periods (2021–2040 and 2041–2060). By revealing the potential distributions of 10 highly-invasive termite species, we identify, at a global scale, potential high-risk areas in the context of climate change, land-use change and increasing connectivity. Our study not only provides information for preventative strategies, but also furnishes a roadmap to help curtailing introduction and early-stage introductions of invasive termite species.

Methods

Species distribution data

In 2013, Evans et al. reported 28 invasive termite species worldwide. Distribution data for these species were extracted from reliable sources including Global Biodiversity Information Facility (GBIF 2024), Sistema de Informação sobre a Biodiversidade Brasileira (SiBBr 2024) and the University of Florida Termite Collection (UFTC) curated by Scheffrahn (2019). Of the 28 species, six had less than 30 occurrences after curation (removing duplicates, excluding coordinates with low accuracy and coordinates from countries where the species had not been reported in the literature). Detailed information on the remaining 22 species, including their respective families, feeding groups, nesting types, breeding systems, target damage, native and invaded ranges and spread methods are given in Table 1 (see Suppl. material 2 for occurrences of the 22 initial invasive species and GBIF DOIs). From this subset, we narrowed our focus on the 10 most invasive termites, discarding those with limited spread capacity (e.g. those inhabiting rotten wood) or those lacking recent reports. Six of them belong to the Kalotermitidae family (*Cryptotermes brevis* (Walker, 1853), *Cr. domesticus* (Haviland, 1898), *Cr. dudleyi* (Banks, 1918), *Cr. havilandi* (Sjöstedt, 1900), *Incisitermes immigrans* (Snyder, 1922) and *I. minor* (Hagen, 1858)), three to the Rhinotermitidae family (*Coptotermes formosanus* (Shiraki, 1909), *Co. gestroi* (Wasmann, 1896) and *Reticulitermes flavipes* (Kollar, 1837)) and one from the Termitidae family (*Nasutitermes corniger* (Motschulsky, 1855)). All produce secondary reproductives and consume wood (Evans et al. 2013). All have a life stage in which they nest in a single piece of wood in which the colony is founded. The Kalotermitidae nest within their food source for the entire life of the colony (i.e. single-piece nesting termite; Abe (1987)); the Rhinotermitidae establish their incipient colony inside a piece of wood or at the wood-soil interface before settling in the soil (Ferraz and Cancello 2004; de Lima

et al. 2006); for *Nasutitermes corniger*, the construction of the final carton nest, whether on a tree or on the ground, may follow the establishment of an incipient colony in a piece of wood (Thorne and Haverty 2000). These life-history traits make them particularly good invaders (Evans et al. 2013).

The curation process of our ten species yielded an average of 313 occurrences per species (Table 1). Three sets of 1000 randomly selected pseudo-absence points were generated for each species using Biomod2 version 4.2-4 package (Thuiller et al. 2009) in the software R version 4.2.0 (R Core Team 2022). These pseudo-absence points were chosen with equal weighting for both presence and absence, following the methodology described by Barbet-Massin et al. (2012).

Explanatory variables

Explanatory varisables were standardised to the same resolution (0.25°, the resampling was done using the nearest-neighbour algorithm), dimensions (*nrow* = 600, *ncol* = 1440), extent (*xmin* = -180°, *xmax* = 180°, *ymin* = -60°, *ymax* = 90°) and format (WGS84 EPSG:4326) using the software QGIS (QGIS 2023). For each species, a raster stack was built with explanatory variables using the package raster_3.6-14 (Hijmans et al. 2015).

Climatic variables

To determine the current distribution of species, we obtained 19 bioclimatic variables from Worldclim 2.1 (Fick and Hijmans 2017) at 2.5 min resolution. These variables were then standardised (same resolution, dimensions, extent and format) using QGIS, as described earlier. To select the most influential variables for each species, we assessed variable importance using six different algorithms through Biomod2. The six algorithms were selected out of the ten available algorithms in the package, based on their strength and widespread usage: Flexible Discriminant Analysis (FDA, Hastie et al. (1994)), Random Forests (RF, Breiman, (2001)), Maximum Entropy from the maxnet version 0.1.4 package (MAXNET, Phillips et al. (2004); Phillips et al. (2017)), Generalised Additive Model (GAM, Hastie and Tibshirani (1986)), Generalised Linear Model (GLM, Nelder and Wedderburn (1972)) and Generalised Boosting Model (GBM, Bühlmann and Hothorn (2007)). The mean importance values were calculated and only the top two variables, which exhibited the highest importance and were uncorrelated (with a Pearson correlation coefficient of less than 0.70, Suppl. material 1: S1), were selected for each species to avoid autocorrelation. Details of the selected variables can be found in Suppl. material 1: S2.

For future climate projections, we accessed several global climate models (GCMs) from the sixth Coupled Model Intercomparison Project (CMIP6; Eyring et al. (2016)) through Worldclim 2.1, also at a 2.5 min resolution. Each CMIP6 GCM has its own strengths and limitations due to differences in its structure, parameterisation, initial condition settings and climate representation (Wang et al. 2021). For this reason, we used three different GCMs (EC-Earth3-Veg-LR, HadGEM3-GC31-LL and MIROC6), based on forcing data availability and representation of the CMIP6. To account for different climate change scenarios and time periods, we selected three combinations. The SSP2-4.5 scenario ("middle of the road": extrapolation of past and current global development into the future; under this scenario, temperatures rise by 2.7 °C by the end of the century) was chosen

for the 2021–2040 (20 years' average) and 2041–2060 time periods. Additionally, we selected the SSP5-8.5 scenario ("fossil-fuelled development": global markets and development, based on fossil fuel resources; under this scenario, current CO_2 emissions levels roughly double by 2050 and warming could reach 4.4 °C in 2100) for the 2041–2060 period to consider a more pessimistic outlook (Riahi et al. 2017). For each scenario and variable, the grid-cell mean was computed amongst the three GCMs to reduce differences between the GCMs. The variables were then standardised (same resolution, dimensions, extent and format) using QGIS, as described earlier. To maintain consistency in the species distribution modelling, we used the same two bioclimatic variables that were chosen for each species' present distribution to model their future distribution.

Land-cover variables

We incorporated land-cover information to capture the habitat preferences of the selected termite species. Land-cover layers were obtained from the Land-Use Harmonization 2 (LUH2) project (Hurtt et al. 2020). This dataset includes 12 layers potentially relevant for termites (See Suppl. material 1: S3 for details). Moreover, each of these layers is available for different years under different shared socioeconomic pathways (SSPs). To align with the bioclimatic variables, we downloaded the 12 layers for four scenarios as similarly as possible: current (SSP2-4.5, year 2023), SSP2.4-5 2021–2040 (SSP2.4-5, year 2040), SSP2.4-5, 2041–2060 (SSP2.4-5, year 2060) and SSP5.8-5 2041–2060 (SSP5.8-5 year, 2060). Like the bioclimatic variables, the land-cover layers were standardised (same resolution, dimensions, extent and format) using QGIS, following the method described earlier. To identify the most influential land-cover variables for each termite species, we applied the variable importance command from the Biomod2 package, using the same set of algorithms as before. The mean importance values were calculated and only the top two variables with a Pearson correlation coefficient of less than 0.70 were selected for each species. This approach ensured that the chosen variables were not strongly correlated with each other, thus avoiding redundancy and maintaining model robustness (Suppl. material 1: S1, S3). For future species distribution modelling, we used the same land-cover layers that were chosen for each species' present distribution.

Connectivity (trade, transport and demography) variables

Socioeconomic variables, such as distance to airports, seaports and human density, are the most significant factors determining the distribution of global invasive species after climatic variables and habitat characteristics (Bellard et al. 2016). Looking ahead, trade and transport, climate change and socioeconomic activities are poised to become the main drivers of biological invasions (Essl et al. 2020). Termites' invasions are typically human-induced, owing to their reliance on wood, a globally-traded commodity. While cargoes and commercial boats containing wood were historically primary vectors for termite invasions (Gay 1969), biosecurity measures have now largely mitigated this risk (Scheffrahn 2023). However, the ten invasive species are likely invading new regions via private vessels such as yachts and sailing boats and, also, in the case of the Kalotermitidae, through the transportation of infested furniture (Scheffrahn 2023; Chouvenc, personal communication, January 2024; Table 1).

Table 1. Invasive termite species with more than 30 occurrences after curation. Provided are the family, the feeding group, the nesting type, the breeding system when known, the damage targets, the native and invaded ranges, as well as their spread methods. The feeding groups are as follows: Type I, protist-dependent termites, mainly wood and grass feeders; Type II, Termitidae, litter and fungus growing wood feeders. The nesting type are as follows: single-piece, i.e. living, nesting and eating in a single piece of wood; intermediate-piece, i.e. starting as a single-piece nester, but then searching for other pieces of wood and changing nest; and separate-piece, i.e. building a nest separated from the food. The colony family structures are classified into: simple family (single pair of monogamous primary reproductives, SF), extended family (multiple secondary reproductives descending from a simple family, EF) or mixed family (more complex genotypes than possible if they are all descended from a primary reproductive pair, MF). Only the species in bold were kept for the study because of their high spread capacity.

Family and species	Short name	Occurrences after curation	Feeding group (Donovan et al. 2001)	Nesting type (Abe 1987)	Secondary reproductives (Evans et al. 2013)	Breeding system (Vargo 2019)	Important pest (Rust and Su 2012)	Damage targets	Native range	Invaded range	Spread methods and risk	References for native and invaded range, and spread methods
Mastotermitidae												
Mastotermes darwiniensis (Froggatt, 1897)	Mdar	50	I	Intermediate-piece	Yes	SF, EF and MF	Yes	Buildings, horticultural and forest trees, plastic	Australia	New Guinea	From imported logs of Eucalyptus and hardwood logs from Australia in the last centuries, but now low risk mainly through live potted plants	Gay (1969); Evans et al. (2013); Lenz et al. (2013); Chouvenc, personal communication, January 2024
Archotermopsidae												
Porotermes adamsoni (Froggatt, 1897)	Pada	101	I	Single-piece	Yes	?	No	Sawn timber, dead trees and living trees (Eucalyptus)	Australia	New Zealand	From imported second-hand railroad ties from Australia in the last centuries, but now low risk mainly through live potted plants	Pearson et al. (2010); Evans et al. (2013); Chouvenc, personal communication, January 2024
Zootermopsis angusticollis (Hagen, 1858)	Zang	690	I	Single-piece	Yes	?	No	Rotten wood	North America	Hawaii	Unknown, as it feeds on rotten wood which is not a great commodity, low risk	Evans et al. (2013)
Zootermopsis nevadensis (Hagen, 1874)	Znev	54	I	Single-piece	Yes	MF	No	Rotten wood	US	Japan	Unknown, as it feeds on rotten wood which is not a great commodity, low risk	Evans et al. (2013); Yashiro et al. (2018)
Kalotermitidae												
Cryptotermes brevis (Walker, 1853)	Cbre	467	I	Single-piece	Yes	?	Yes	Buildings	Coastal Chile, Peru	S and N America, W Africa, Azores, Australia (Brisbane), Fiji, Pacific and Atlantic islands, Egypt	From furniture, wooden articles, pallets, dunnage, sailboats, ships and planes, high risk	Helal and Ali (1982); Scheffrahn et al. (2009); Evans et al. (2013); Haigh et al. (2023)
Cryptotermes domesticus (Haviland, 1898)	Cdom	32	I	Single-piece	Yes	?	Yes	Buildings	SE Asia	China, Taiwan, Japan, Australia, Pacific Ocean, Polynesia	Intercepted in private vessels, high risk	Scheffrahn and Crowe (2011); Evans et al. (2013)
Cryptotermes dudleyi (Banks, 1918)	Cdud	50	I	Single-piece	Yes	?	Yes	Buildings	SE Asia	India, Bangladesh, Indian Ocean, East Africa, Australia, Micronesia, South America	Intercepted in private vessels, high risk	Scheffrahn and Crowe (2011); Evans et al. (2013)

Family and species	Short name	Occurrences after curation	Feeding group (Donovan et al. 2001)	Nesting type (Abe 1987)	Secondary reproductives (Evans et al. 2013)	Breeding system (Vargo 2019)	Important pest (Rust and Su 2012)	Damage targets	Native range	Invaded range	Spread methods and risk	References for native and invaded range, and spread methods
Cryptotermes havilandi (Sjöstedt, 1900)	*Chav*	42	I	Single-piece	Yes	?	Yes	Buildings	West Africa	E Africa, India, S America, West Indies and Indian islands	Probably from wooden rafts or boats from Madagascar long time ago and now probably in boats like other *Cryptotermes* species, high risk	Gay (1969); Evans et al. (2013); Chouvenc, personal communication, January 2024
Glyptotermes brevicornis (Froggatt, 1897)	*Gbre*	55	I	Single-piece	Yes	?	No	Non-significant	Australia	New Zealand and Fiji	Very limited spread, low risk	Evans et al. (2013)
Incisitermes immigrans (Snyder, 1922)	*Iimm*	40	I	Single-piece	Yes	?	No	Buildings	Central and South America	Pacific Ocean, Hawaii, Japan	From infested wood from a wrecked schooner in the last centuries and now probably through movement of furniture like *I. minor*, high risk	Gay (1969); Evans et al. (2013)
Incisitermes minor (Hagen, 1858)	*Imin*	311	I	Single-piece	Yes	SF, EF and MF	Yes	Buildings	South-western US and northern Mexico	Eastern US, Canada, China, Pacific Ocean, Japan	From wooden chests, furniture, and grape boxes from US West Coast and now through movement of furniture, high risk	Gay, 1969; Evans et al. (2013); Chouvenc, personal communication, January 2024

Rhinotermitidae

Family and species	Short name	Occurrences after curation	Feeding group (Donovan et al. 2001)	Nesting type (Abe 1987)	Secondary reproductives (Evans et al. 2013)	Breeding system (Vargo 2019)	Important pest (Rust and Su 2012)	Damage targets	Native range	Invaded range	Spread methods and risk	References for native and invaded range, and spread methods
Coptotermes acinaciformis (Froggatt, 1898)	*Caci*	464	I	Intermediate-piece	Yes	?	Yes	Buildings, orchard trees, rubber trees, oil palms, plastic	Australia	New Zealand	From railroad ties and telephone poles from Australia in the last centuries, but now low risk mainly through live potted plants	Miller (1940); Lenz et al. (2013); Evans et al. (2013); Chouvenc, personal communication, January 2024
Coptotermes formosanus (Shiraki, 1909)	*Cfor*	367	I	Intermediate-piece	Yes	SF and EF	Yes	Buildings, sugarcane, plastic	China and Taiwan	Japan, US, Israel	From recycled railroad ties, potted plants, furniture and private vessels, high risk	Atkinson et al. (1993); Jenkins et al. (2002); Messenger et al. (2002); Evans et al. (2013); Tonini et al. (2014); Chouvenc et al. (2016); Evans et al. (2019); Scheffrahn et al. (2020)
Coptotermes frenchi (Hill, 1932)	*Cfre*	132	I	Intermediate-piece	Yes	?	Yes	Buildings, eucalyptus trees	Australia	New Zealand	From railroad ties and imported logs from Australia in the last centuries, but now low risk mainly through live potted plants	Gay (1969); Evans et al. (2013); Tonini et al. (2014)
Coptotermes gestroi (Wasmann, 1896)	*Cges*	285	I	Intermediate-piece	Yes	?	Yes	Buildings, pine trees, plastic	SE Asia	Taiwan, Pacific Ocean, Micronesia, Mexico, Florida, West Indies, Brazil	Intercepted in private vessels, high risk	Scheffrahn and Crowe (2011); Tonini et al. (2014); Evans et al. (2013); Chiu et al. (2016)
Heterotermes cardini (Snyder, 1924)	*Hcar*	320	I	Intermediate-piece	Yes	SF, EF and MF	No	Buildings	Bahamas, Panama, Cuba, Jamaica, Cayman Islands, Panama Colombia	US (Florida)	Probably shipboard infestations in the last centuries and now private vessels, medium risk	Szalanski et al. (2004); Evans et al. (2013); Carrijo et al. (2020)

Family and species	Short name	Occurrences after curation	Feeding group (Donovan et al. 2001)	Nesting type (Abe 1987)	Secondary reproductives (Evans et al. 2013)	Breeding system (Vargo 2019)	Important pest (Rust and Su 2012)	Damage targets	Native range	Invaded range	Spread methods and risk	References for native and invaded range, and spread methods
Heterotermes convexinotatus (Snyder, 1924)	*Hcon*	460	I	Intermediate-piece	Yes	SF, EF and MF	Yes	Crops and buildings	Southern Mexico, Nicaragua, northern Colombia, Panama, northern Venezuela	Puerto Rico, Haiti, Antigua, Barbados, Martinique, Guadeloupe, Saint Kitts, Saint Martin, Galapagos	Probably shipboard infestations in the last centuries and now private vessels, medium risk	Szalanski et al. (2004); Evans et al. (2013)
Heterotermes tenuis (Hagen, 1858)	*Hten*	449	I	Intermediate-piece	Yes	SF, EF and MF	Yes	Crops and buildings	Argentina, Brazil, Bolivia, Colombia, Costa Rica, Ecuador, Guianas, Panama, Paraguay, Peru, Venezuela	West indies	Probably shipboard infestations in the last centuries and now private vessels, medium risk	Szalanski et al. (2004); Evans et al. (2013)
Reticulitermes flavipes (Kollar, 1837)	*Rfla*	812	I	Intermediate-piece	Yes	SF, EF and MF	Yes	Buildings	Eastern US, northern Bahamas	Canada, Europe, South America, Easter Island	From imported timbers and from railroad ties from North America in the last centuries, but now probably through budding in infested furniture, high risk	Gay (1969); Scheffrahn et al. (2006); Evans et al. (2013); Baudouin et al. (2018); Perdereau et al. (2019)
Reticulitermes grassei (Clément, 1977)	*Rgra*	33	I	Intermediate-piece	Yes	SF, EF and MF	No	Buildings and oak trees	South-western Europe (France and Spain)	Britain, Azores	Very limited spread, medium risk	Evans et al. (2013)
Termitidae												
Nasutitermes corniger (Motschulsky, 1855)	*Ncor*	726	II	Separate-piece	Yes	MF	Yes	Buildings, ornamental trees	Central, S America, West Indies	New Guinea, Florida	Intercepted in private vessels, high risk	Scheffrahn et al. (2002); Scheffrahn et al. (2005); Scheffrahn and Crowe (2011); Evans et al. (2013)
Termes hispaniolae (Banks, 1918)	*This*	420	II	Separate-piece	Yes	?	No	No damage	Coasts of Central and S America	West indies	Intercepted in shipments of firewood in the last century, low risk	Gay (1969); Evans et al. (2013)

To address these dynamics, we selected three connectivity variables (four if including urban areas): Accessibility to Cities (ATC, trade and transport related, Weiss et al. (2018)), human population (POP, demography related, Jones and O'Neill (2016)) and a leisure vessels variable (LVE, transport related, Cerdeiro et al. (2020)). The LVE variable draws from a comprehensive 6-layer dataset containing various vessel types, such as commercial and fishing ships, as well as recreational vessels (LVE) like yachts and sailboats.

The ATC layer quantifies the time it takes to travel to the nearest urban area through foot, roads, railways and rivers, as of 2015 (Weiss et al. 2018), providing valuable insights into the pathways through which invasive termite species can be introduced. While future projections are not yet available, the ATC layer was used for the current and future projections.

POP gives a more precise representation of densely populated areas compared to the urban variable, as it considers the number of inhabitants rather than solely the footprint of a building (Jones and O'Neill 2016). Both ATC and POP are anticipated to correlate with furniture transportations, as denser and more connected urban centres facilitate increased exchange. Projection of POP into future scenarios align with land-cover variables, employing the same scenarios and years. For the current year, the SSP2 year 2020 was used, as it is the closest to the present.

The LVE variable (downloaded from the Worldbank.org database) delineates leisure vessels density based on AIS (automatic identification system) positions of leisure vessels between January 2015 and February 2021, with higher densities observed in major marinas, influencing model outcomes (Cerdeiro et al. 2020). As these boats frequently linger in marinas for extended periods, reproductive individuals have ample opportunity to emerge and take flight inland towards illuminated areas (Scheffrahn and Crowe 2011; Hochmair et al. 2023; Scheffrahn 2023). Moreover, leisure vessels, particularly yachts, may traverse oceans via specialised transport vessel (DYT Yacht Transport 2024), thereby extending their potential impact on dispersal patterns. Although no future projections are available, the variable was used for both current and future projections.

All three layers (ATC, POP and LVE) were standardised (same resolution, dimensions, extent and format) using QGIS, following the methodology described earlier. The Pearson correlation analysis (refer to Suppl. material 1: S1) did not result in the elimination of any of the three layers, as none had a correlation higher to 0.70. By integrating these three connectivity variables (four if including urban areas) into our modelling framework, we aim to capture the intricate interplay between private vessels, human populations, furniture exchanges and the potential distribution patterns of invasive termite species.

Elevation variable

Termite diversity typically decreases with increasing elevation, primarily due to lower temperatures that result in unsuitable habitats for warm-adapted species (Gathorne-Hardy et al. 2001; Palin et al. 2011; Chiu et al. 2019). However, higher elevations are also associated with lower air pressure, increased solar radiation, steeper slopes and higher wind speeds, all of which can significantly impact terrestrial insects (Hodkinson 2005). Additionally, elevation has been observed to influence the shape of termite nests in certain species (Jamilu Bala Ahmed et al. 2019). Given these findings, elevation holds the potential to be a significant pre-

dictor variable for the distribution of invasive termites. Consequently, an elevation (ELE) layer was acquired from earthenv.org at a 1 km resolution and in a median aggregated format (Amatulli et al. 2018). The layer was then standardised (same resolution, dimensions, extent and format) using the same methodology described earlier in QGIS. The elevation variable had no strong correlation (> 0.70) with the other variables (Pearson correlation analyses, refer to Suppl. material 1: S1), validating its inclusion in the models.

Modelling and evaluation

The entire modelling and evaluation process was conducted in R4.2.0 using the Biomod2 4.2-4 package. We performed modelling analyses by integrating bioclimatic, land-use, connectivity and elevation variables into our models. Additionally, we ran models exclusively using bioclimatic variables to assess outcomes and discern any divergences. The same algorithms (FDA, RF, MAXNET, GAM, GLM, GBM) as described earlier were used for all the modelling. For model training, only 75% of the randomly-selected occurrences were utilised, while the remaining 25% were kept for model evaluation. The performance of the models was assessed using two metrics: True Skill Statistic (TSS, Allouche et al. (2006)) and Area Under a Receiver Operating Characteristic (ROC or AUC, Hanley and Mc-Neil (1982)). To validate the models, a 5+1-fold cross-validation was conducted for each species. This resulted in a total of 108 models (six algorithms multiplied by 5+1 cross-validations multiplied by three pseudo-absence samplings) fitted for each species, considering both current and future shared socioeconomic pathways. The importance (i.e. the contribution to the model) of each variable (climatic, land-cover, connectivity and elevation) for each species was evaluated using the variable importance command from Biomod2.

Ensemble modelling, which combines individual forecasts into a consensus projection (Araújo and New 2007), has become a popular technique in species distribution modelling (Hao et al. 2019). However, it may not be always the best approach if all default settings of Biomod2 are chosen, as it can lead to underperforming models compared to well-tuned individual models (Valavi et al. 2022). Therefore, except for MAXNET, FDA and GBM, the default settings of Biomod2 were not used. For RF, downscaled performance is improved by adding the sampsize option and ntrees was set to 1000 as recommended by Valavi et al. (2022). GAM performed best using the GAM_mgcv algorithm, the binomial family (logit) and the REML method (Pedersen et al. 2019). GLM utilised the binomial family (logit) (Hastie et al. 2001). To ensure that only high-performing individual models were included in the ensemble modelling, a threshold of 0.75 was set for the TSS metric. The weighted average method was employed to create the consensus model, as it provides more robust predictions alongside the mean compared to other methods (Marmion et al. 2009). Finally, the same metrics (TSS and ROC) used for the individual models were used to assess the quality of the final consensus model. For ROC, models can be considered poor for values in the range 0.5–0.7, fair in the range 0.7–0.9 and excellent when the value ranges between 0.9 and 1 (Swets 1988). For TSS, models can be considered poor for values ranging from 0.2 to 0.5, useful when ranging from 0.6 to 0.8 and can be considered good to excellent when ranging from 0.8 to 1 (Coetzee et al. 2009).

Evaluating the range shift between the present and the future

To facilitate the visual comparison between present and future scenarios, the range size function from Biomod2 was used instead of relying on multiple maps. This function computes the number of pixels that are lost, stable or gained, along with their relative proportions, when comparing two species distribution models. To perform this analysis, the current and future ensemble models were transformed into binary predictions (absence: 0 or presence: 1) by applying an optimised threshold derived from TSS (Thuiller et al. 2009). This approach allowed us to generate a single map that delineates the regions where each species is contracting, stabilising, expanding or absent. Additionally, using Biomod2, the net increase (percentage of pixels predicted to be gained compared to the number of pixels currently occupied) and decrease (percentage of pixels currently occupied and predicted to be lost) were calculated for each species. This methodology provides a clear representation of the spatial dynamics for each species and quantifies the net changes in terms of percentage for each species, offering valuable insights into the projected shifts in their distributions.

Mapping high-risk invasion area

To delineate potential high-risk invasion areas, the same methodology as outlined in the previous section was used. However, "lost" and "absent" pixels were converted to 0, while "stable" and "increase" pixels were converted to 1. This adjustment enabled the summation of values for each species across all pixels, providing an estimate of the potential number of species in each pixel under the selected scenario.

Results

Models' performance and variables' importance

The evaluation process supports the robustness and accuracy of the models in predicting species distributions. For ROC, all the individual models could be considered excellent (0.900–1), ranging from 0.968 to 1, while all the ensemble models were close to perfect, ranging from 0.986 to 1 with an excellent average of 0.996. For TSS, all the individual models could be considered good to excellent (0.800–1), ranging from 0.819 to 0.999, while all the ensemble models were good to excellent ranging from 0.879 to 0.994 with an excellent average of 0.958 (Suppl. material 1: S4).

The analysis of variable importance revealed that bioclimatic variables were overall the most important predictors, followed by our four connectivity variables. In contrast, the significance of elevation and land-cover variables (excluding urban land) appears comparatively lower than other variables (Fig. 1, Table 2). The combined use of bioclimatic, land-use, connectivity and elevation variables as predictors refine our projections by reducing by an average of 313% the areas suitable to the establishment of all termite species under study (Table 3).

Amongst the top three most important variables, a bioclimatic variable ranked first for six species and urban land for four species. Ranking second in importance, bioclimatic factors held for six species, whereas urban land held for two species. Accessibility to Cities (ATC) and elevation (ELE) held this position for one species. Lastly, the third-rank variable category encompassed bioclimatic factors for four
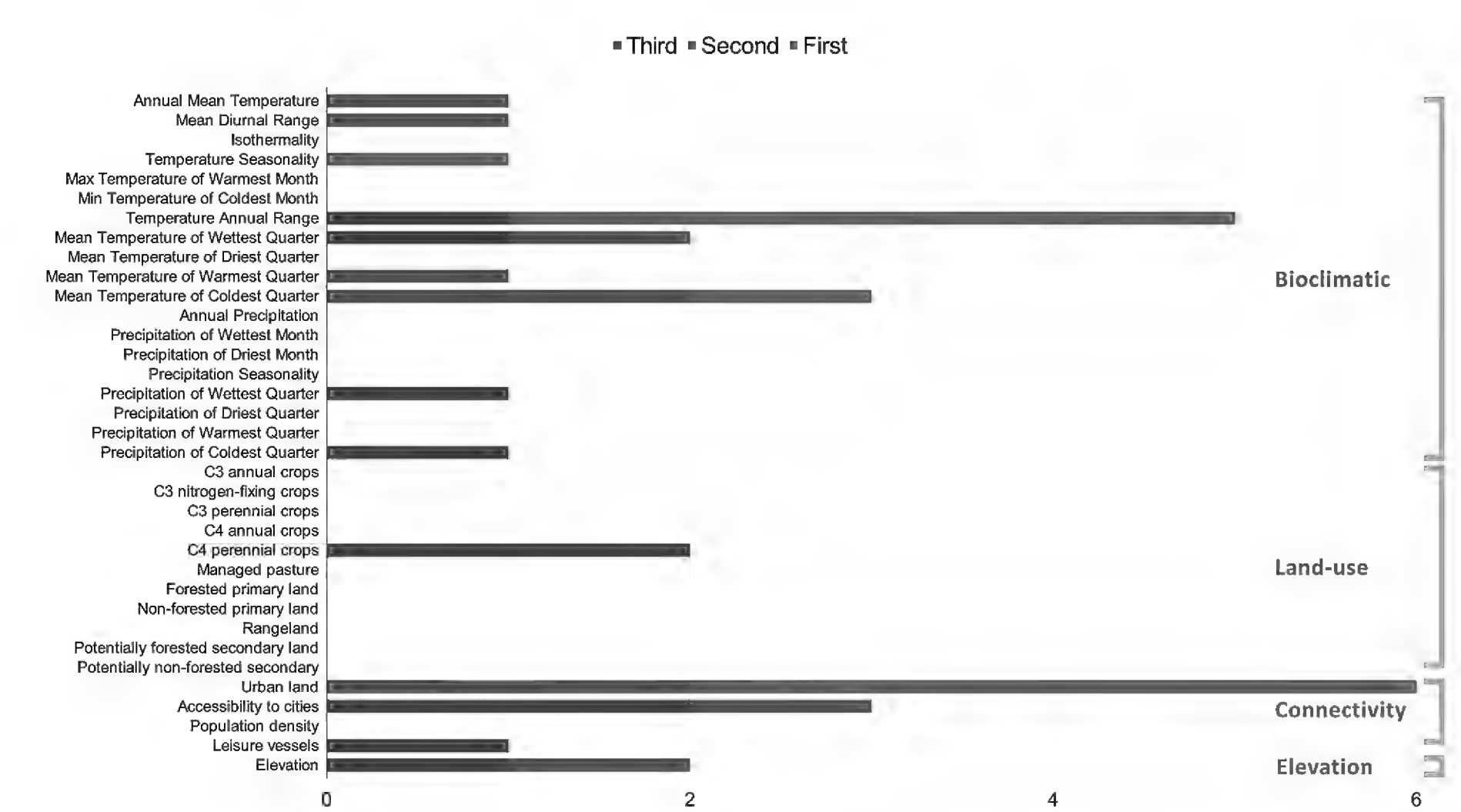
Figure 1. Number of times each variable was identified as the most important (First), second most important (Second) and third most important (Third) for each species.

species, C4 perennial crops for two species, ATC for two species, leisure vessels (LVE) and elevation for one species (Fig. 1). Our results underscore the prevailing role of bioclimatic variables and the substantial influence of trade, transport and demography factors (i.e. the connectivity variables) in shaping the distribution patterns of invasive termite species. Concerning the land-cover variables (excluding urban land), only one variable, C4 perennial crops, managed to reach the top three positions. In addition to several bioclimatic and most land-cover variables, the population variable (POP) failed to secure a position in the top three average contributions. Amongst the bioclimatic variables, those linked to temperature held a significant presence in the top three, occurring seven times more frequently as variables tied to precipitation (Fig. 1, Table 2, Suppl. material 1: S5 for the response curves).

Potential current habitat suitability

The majority of the ten invasive species demonstrate significant potential for occupying a wide range of habitats for the current climate conditions and socioeconomic development. Although no overarching trends apply to all our species, some preferences can be observed with our models. For instance, species such as *Cryptotermes brevis, Cryptotermes domesticus, Incisitermes immigrans, Incisitermes minor, Coptotermes formosanus, Coptotermes gestroi* and *Reticulitermes flavipes* all show preference for large and well-connected urban areas, while *Cryptotermes dudleyi, Cryptotermes havilandi* and *Nasutitermes corniger* appear to be slightly more restricted to environments resembling their native habitats (Table 3, Suppl. material 1: S6 for all the maps). Below, we will describe the results of the models for each species, focusing solely on their statistical performance without considering their ecological context or the actual conditions of their habitats. For a deeper analysis incorporating these factors, please refer to the Discussion section.

Table 2. Average contribution of each predictive variable to the model for each species. In total, eight variables (2/19 for bioclimatic and 2/12 for land-use) were chosen for each species (see Suppl. material 1: S2 and S3 for further details). The three highest values are highlighted. The name of the termite species is as follows: *Cryptotermes brevis*, Cbre; *Cryptotermes domesticus*, Cdom; *Cryptotermes dudleyi*, Cdud; *Cryptotermes havilandi*, Chav; *Incisitermes immigrans*, Iimm; *Incisitermes minor*, Imin; *Coptotermes formosanus*, Cfor; *Coptotermes gestroi*, Cges; *Reticulitermes flavipes*, Rfla; and *Nasutitermes corniger*, Ncor.

Variable	Kalotermitidae						Rhinotermitidae			Termitidae
	Cbre	*Cdom*	*Cdud*	*Chav*	*Iimm*	*Imin*	*Cfor*	*Cges*	*Rfla*	*Ncor*
Bioclimatic										
Annual Mean Temperature							0.159			
Mean Diurnal Range			0.218							
Isothermality										
Temperature Seasonality			0.407							
Max Temperature of Warmest Month										0.086
Min Temperature of Coldest Month										
Temperature Annual Range		0.407		0.572	0.662				0.090	0.484
Mean Temperature of Wettest Quarter		0.354		0.311						
Mean Temperature of Driest Quarter										
Mean Temperature of Warmest Quarter									0.177	
Mean Temperature of Coldest Quarter	0.203					0.164		0.2853		
Annual Precipitation										
Precipitation of Wettest Month					0.088					
Precipitation of Driest Month	0.038									
Precipitation Seasonality										
Precipitation of Wettest Quarter							0.086			
Precipitation of Driest Quarter								0.047		
Precipitation of Warmest Quarter										
Precipitation of Coldest Quarter						0.121				
Land-use										
C3 annual crops					0.097					0.029
C3 nitrogen-fixing crops										
C3 perennial crops										
C4 annual crops										
C4 perennial crops			0.161	0.071						0.057
Managed pasture										
Forested primary land		0.121				0.061			0.061	
Non-forested primary land	0.015		0.067					0.025		
Rangeland				0.101			0.024			
Potentially forested secondary land										
Potentially non-forested secondary land										
Connectivity										
Urban land	0.284	0.090			0.252	0.543	0.468	0.233	0.360	
Accessibility to cities	0.119	0.263	0.111	0.010	0.152	0.065	0.014	0.159	0.073	0.095
Population density	0.020	0.116	0.077	0.057	0.079	0.025	0.011	0.045	0.028	0.012
Leisure vessels	0.019	0.060	0.029	0.148	0.019	0.004	0.003	0.004	0.006	0.007
Elevation										
Elevation	0.014	0.403	0.137	0.085	0.064	0.018	0.085	0.232	0.050	0.016

Kalotermitidae

Cryptotermes brevis, originating from Coastal Chile and Peru, has expanded its distribution to encompass North and South America, western Africa, the Azores, Australia (around Brisbane) and numerous Pacific and Atlantic islands (Table 1). In addition to its native range, model analysis indicates current suitability predominantly in the urban areas of eastern US, as well as in the West Indies, throughout patches of Central and South America and around Lagos, Lake Victoria and Lower Egypt in Africa where it has already established itself. In Europe and Asia, the

Table 3. Summary of the main results. Native range, invaded range, potential current habitat suitability, range shift between our models and our models using only bioclimatic variables, potential lost and new ranges for the most pessimistic scenario and range shift for each scenario according to our models for each species.

Family and species	Native range	Invaded range	Potential current habitat suitability (See Suppl. material 1: S6 for maps)	Differences between multifactorial modelling and bioclimatic modelling	Potential lost and new ranges for SSP5-8.5 2041–2060 compared to potential current habitat (See Suppl. material 1: S6 for maps)	Range shift between current and:		
						SSP2-4.5 2021–2040	SSP2-4.5 2041–2060	SSP5-8.5 2041–2060
Kalotermitidae								
Cryptotermes brevis	Coastal Chile, Peru	S and N America, W Africa, Azores, Australia (Brisbane), Fiji, Pacific and Atlantic islands, Egypt	Mainly cities of eastern US, West Indies, big cities of Central and South America, around Lagos, Lake Victoria and Lower Egypt. Big port towns in Europe, large economic areas of Asia and a few cities of the eastern coast of Australia	34.79%	New ranges: deeper into the US, Europe, India, China, and Japan, western Australia. Some lost ranges: Central America, Brazil, India, Indonesia	5.47%	3.12%	-11.85%
Cryptotermes domesticus	SE Asia	China, Taiwan, Japan, Australia, Pacific Ocean, Polynesia	SE Asia, southern coast of China, south-eastern coast of India, Japan, Taiwan, Central America, West Indies, Florida and major cities of the Guinean coasts	-1175.27%	New ranges: deeper into SE Asia, eastern and western coasts of Africa, Florida, Central and South America	-22.66%	19.15%	81.21%
Cryptotermes dudleyi	SE Asia	India, Bangladesh, Indian Ocean, East Africa, Australia, Micronesia, South America	SE Asia, southern coast of China, India, Japan, Taiwan, Central America, South America, West Indies, Florida and major cities of the Guinean coasts	-47.73%	Lost ranges: mainly in South America, western Africa and India	-37.49%	-60.96%	-29.22%
Cryptotermes havilandi	West Africa	E Africa, India, S America, West Indies and Indian islands	Western Africa, West Indies, Central and coastal South America, SE Asia, Sri Lanka, southern tip of India	-120.91%	New ranges: deeper into Central and South America, Africa, India and SE Asia	16.11%	47.04%	105.34%
Incisitermes immigrans	Central and S America	Pacific Ocean, Hawaii, Japan	Central and S America, western Africa, SE Asia	-256.91%	New ranges: large urban areas of the US and Australia; deeper into Africa and SE Asia. Lost ranges: in some parts of South America and western Africa	-17.17%	2.62%	17.11%
Incisitermes minor	South-western US and northern Mexico	Eastern US, Canada, China, Pacific Ocean, Japan	Large cities of North America, Europe, around the Mediterranean Sea and important economic areas of Asia and Australia	-168.78%	New ranges: deeper into the US, Europe, Middle-East, Australia, China	34.95%	64.44%	80.98%
Rhinotermitidae								
Coptotermes formosanus	China and Taiwan	Japan, US, Israel	Large cities of: south-eastern US, south-eastern China, Japan, India, Indonesia, Australia, Brazil, Argentina, Puerto Rico, Israel and Egypt	-1059.63%	New ranges: large urban areas of the US, Europe, western Africa and deeper into China, Japan, India, Indonesia, Australia, Brazil, Argentina, Israel and Egypt. Lost ranges: in a few places between China and Vietnam	67.88%	77.68%	174.70%
Coptotermes gestroi	SE Asia	Taiwan, Pacific Ocean, Micronesia, Mexico, Florida, West Indies, Brazil	SE Asia, Brazil, West Indies, Florida as well as large economic areas of: south-eastern China, Japan, India, Australia, western Africa. In a few cities of the US and Europe	-216.41%	New ranges: more urban areas of US and Europe, deeper into Central America, South America, Africa, India, China, Japan, SE Asia and Australia	38.96%	54.34%	28.13%
Reticulitermes flavipes	Eastern US, northern Bahamas	Canada, Europe, South America, Easter Island	Eastern and western US, southern South America, most of Europe and the coasts of the Mediterranean Sea, most of eastern China, Korea, Japan and the main cities of Australia	-72.68%	New ranges: deeper into the US, Europe, southern South America and Africa, southern Australia, Japan. Lost ranges: US (Texas, Louisiana, Arkansas, Mississippi), northern Africa, China	38.26%	33.23%	47.25%
Termitidae								
Nasutitermes corniger	Central, S America, West Indies	New Guinea, Florida	Central America, South America, West Indies, Florida, tropical Africa and tropical India as well as SE Asia	-46.24%	Lost ranges: mainly South America but also in some parts of Central America and tropical Africa	-21.83%	-54.24%	-34.56%

model suggests some suitability in large economic hubs such as major port cities in Europe, the Guangdong-Hong Kong-Macao Greater Bay Area in China, Jakarta and Tokyo. In Australia, suitability is limited to a few cities on the eastern coast where *Cr. brevis* is already established (Table 3, Suppl. material 1: S6).

Cryptotermes domesticus, originates from Southeast Asia and has invaded China, Taiwan, Japan, Australia and Pacific islands (Table 1). Modelling shows significant suitability beyond its native range, particularly along the southern coast of China, south-eastern coast of India and major cities in Japan and Taiwan. Some areas show less likely suitability due to the presence of the mutually exclusive *Cr. brevis* (Scheffrahn et al. 2009), such as Central America, the West Indies, Florida and major cities along the Guinean coasts (Table 3, Suppl. material 1: S6).

Cryptotermes dudleyi, also originating from Southeast Asia, has already invaded India, Bangladesh, Indian Ocean islands, eastern Africa, Australia, Micronesia and South America (Table 1). Modelling suggests current suitability similar to *Cr. domesticus*, but with larger coverage, especially in India (Table 3, Suppl. material 1: S6).

Cryptotermes havilandi, originating from western Africa, has spread to eastern Africa, India, South America, Indian Ocean islands and the West Indies (Table 1). Modelling suggests strong suitability in areas where it has already spread, such as the West Indies and coastal South America, as well as Southeast Asia, Sri Lanka and the southern tip of India (Table 3, Suppl. material 1: S6).

Incisitermes immigrans is native to Central and South America and, though not a structural pest, has been introduced to several Pacific islands, such as the Galapagos, Polynesia, Hawaii and Japan (Table 1). Beyond the native range, modelling reveals primarily suitability in other tropical regions like western Africa and south-eastern Asia (Table 3, Suppl. material 1: S6). Japan shows limited suitability according to the models.

Incisitermes minor, native to south-western USA and northern Mexico, has extended its range to eastern USA, Canada, China, Pacific Islands and Japan in part through the transportation of infested furniture (Chouvenc, personal communication, January 2024, Table 1). In addition to its endemic range, modelling indicates potential suitability in major cities of Europe and around the Mediterranean Sea, as well as in key economic areas of Asia (mainly in China and Japan) and Australia. South America and Africa have high suitability in their largest cities (Table 3, Suppl. material 1: S6). Its spread is ensured by the transportation of infested furniture since *I. minor* does not disperse to new localities by imago flights (Scheffrahn, personal communication, March 2024).

Rhinotermitidae

Originating from China and Taiwan, *Coptotermes formosanus* has established populations in the US, Hawaii, Israel and Japan (Table 1). Beyond its native range, modelling suggests suitability patterns consistent with its current distribution, particularly in large cities in south-eastern US, Japan, Israel and Egypt, with additional areas of concern in the less likely humid tropics like India, Indonesia, Australia, Brazil, Argentina and Puerto Rico (Table 3, Suppl. material 1: S6).

Coptotermes gestroi, native to Southeast Asia, has become invasive in Taiwan, Micronesia, Mexico, Florida, the West Indies, Brazil and several Pacific Islands (Table 1). Beyond the native range, the modelling shows suitability in Brazil, the West Indies and Florida, where it is already present, as well as potential suitability

in major economic centres in China, Japan, Australia and western Africa (Table 3, Suppl. material 1: S6).

Reticulitermes flavipes, a native pest of the eastern US and the northern Bahamas, has been introduced to Canada, Europe, South America and Easter Island (Table 1). Beyond the native range, modelling reveals large suitability in regions where other pestiferous *Reticulitermes* species are present, such as western US, southern South America, most of Europe, the coasts of the Mediterranean Sea, eastern China, Korea, Japan and major cities in Australia (Table 3, Suppl. material 1: S6).

Termitidae

Nasutitermes corniger, a pest native to Central and South America and the West Indies, has spread to Florida and New Guinea (Table 1). Modelling suggests potential suitability across most tropical regions outside its native range, in Africa, India and Southeast Asia (Table 3, Suppl. material 1: S6).

Range shift in a changing climate and socioeconomic development

In the short term (2021–2040) and under the SSP2-4.5 scenario, four species are projected to have a significant (> 20%) expanded range: *I. minor* by 35%, *R. flavipes* by 38%, *Co. gestroi* by 39% and *Co. formosanus* by 68%. In contrast, three species are expected to experience a significant decline in their habitat range: *N. corniger* by 22%, *Cr. domesticus* by 23% and *Cr. dudleyi* by 37%. Three species, *Cr. brevis*, *Cr. havilandi* and *I. immigrans*, are forecast to maintain their current distribution with minimal variations during this period and scenario (Fig. 2, Suppl. material 1: S7).

When considering the long term (2041–2060) under the same SSP2-4.5 scenario, the trend remains consistent, except that one more species, *Cr. havilandi*, is expected to experience a significant range expansion, by 47% instead of the previous 16% observed in the short term (Fig. 2, Suppl. material 1: S7). For most species, the change in range becomes even more pronounced during this later period.

Shifting to a more pessimistic scenario ("fossil-fuelled scenario", SSP5-8.5) reveals a broader impact, with six species significantly increasing their habitat range. *Co. gestroi* is expected to expand by 28%, *R. flavipes* by 47%, *Cr. domesticus and I. minor* by 81%, *Cr. havilandi* by 105% and *Co. formosanus* by 175%. Conversely, *Cr. dudleyi* and *N. corniger* could experience a significant reduction in range, by 29% and 35%, respectively, under this scenario; while *Cr. brevis* could see a slight decrease of 12% (Fig. 2, Suppl. material 1: S7).

Overall, the average range shift is consistently positive for each scenario and increases over time as the combined effects of climate change and socioeconomic developments intensify. Specifically, in the short term (2021–2040 SSP2-4.5), the average range shift is low at 10%. In the long term (2041–2060) under the same scenario, this increases to 19%. In a scenario characterised by higher fossil fuel reliance, the range shift reaches 46% (Suppl. material 1: S7). These percentages represent net changes in terms of pixels and do not offer insights into the specific regions that may be affected in the future. The right side of Fig. 2 addresses precisely this limitation by showing the number of species potentially suitable in each pixel of the map for each scenario. Upon closer examination, regardless of the scenario, it appears clear that major cities and thriving economic hubs are the most at risk, especially in North America, South America, western Africa, Europe
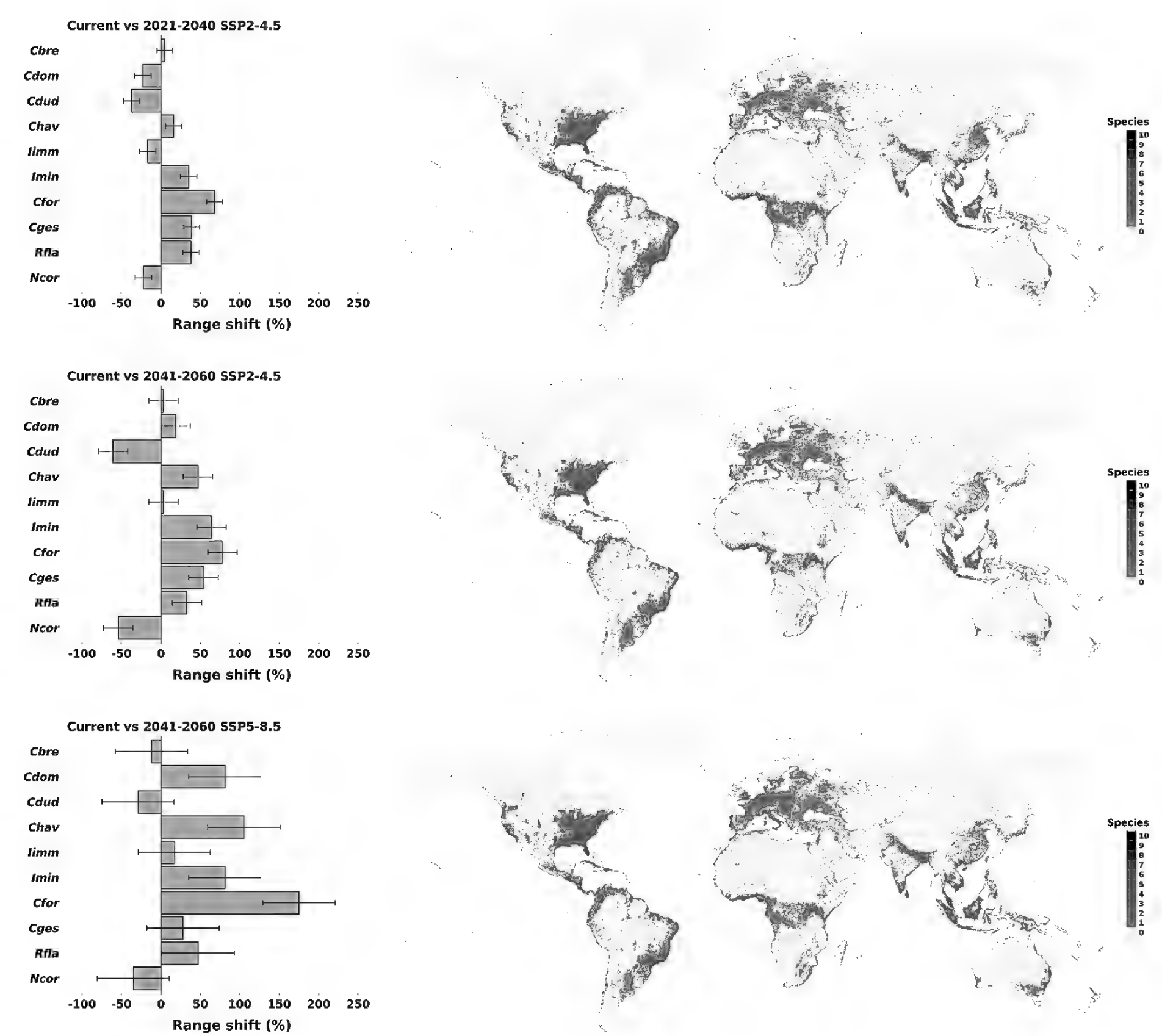
Figure 2. Potential projected range shift (left) and high-risk invasion map (right) for selected periods and socioeconomic-shared pathways.

and the Asia Pacific Region. In these areas, the number of potential species for the worst scenario is between 5 and 10. When focusing on individual countries, several seem to be especially at high risk: the US, Brazil, Nigeria, China, Indonesia, Japan and Australia. These countries could host a substantial number of cities with a high number of invasive species. Nevertheless, all continents have significant areas suitable for more than four species at a time (Fig. 2).

To look at the range shift for each species separately, a comprehensive set of 30 distinct maps providing a visual depiction of the changes for each species, timeframe and shared socioeconomic pathway has been developed (Suppl. material 1: S6). Overall, the trend shows that, under more pessimistic scenarios and over time, species tend to shift towards higher latitudes, both northwards and southwards. Most species are, however, expected to experience a slightly reduced range in lower latitudes (Table 3, Suppl. material 1: S6). For instance, a striking comparison can be made amongst three contrasting species, *Incisitermes minor*, *Reticulitermes flavipes* and *Nasutitermes corniger*. *I. minor*, originating from the south-western US and northern Mexico, has spread likely through the transportation of infested

Incisitermes minor: Current vs 2041-2060 SSP5-8.5

Reticulitermes flavipes: Current vs 2041-2060 SSP5-8.5

Nasutitermes corniger: Current vs 2041-2060 SSP5-8.5
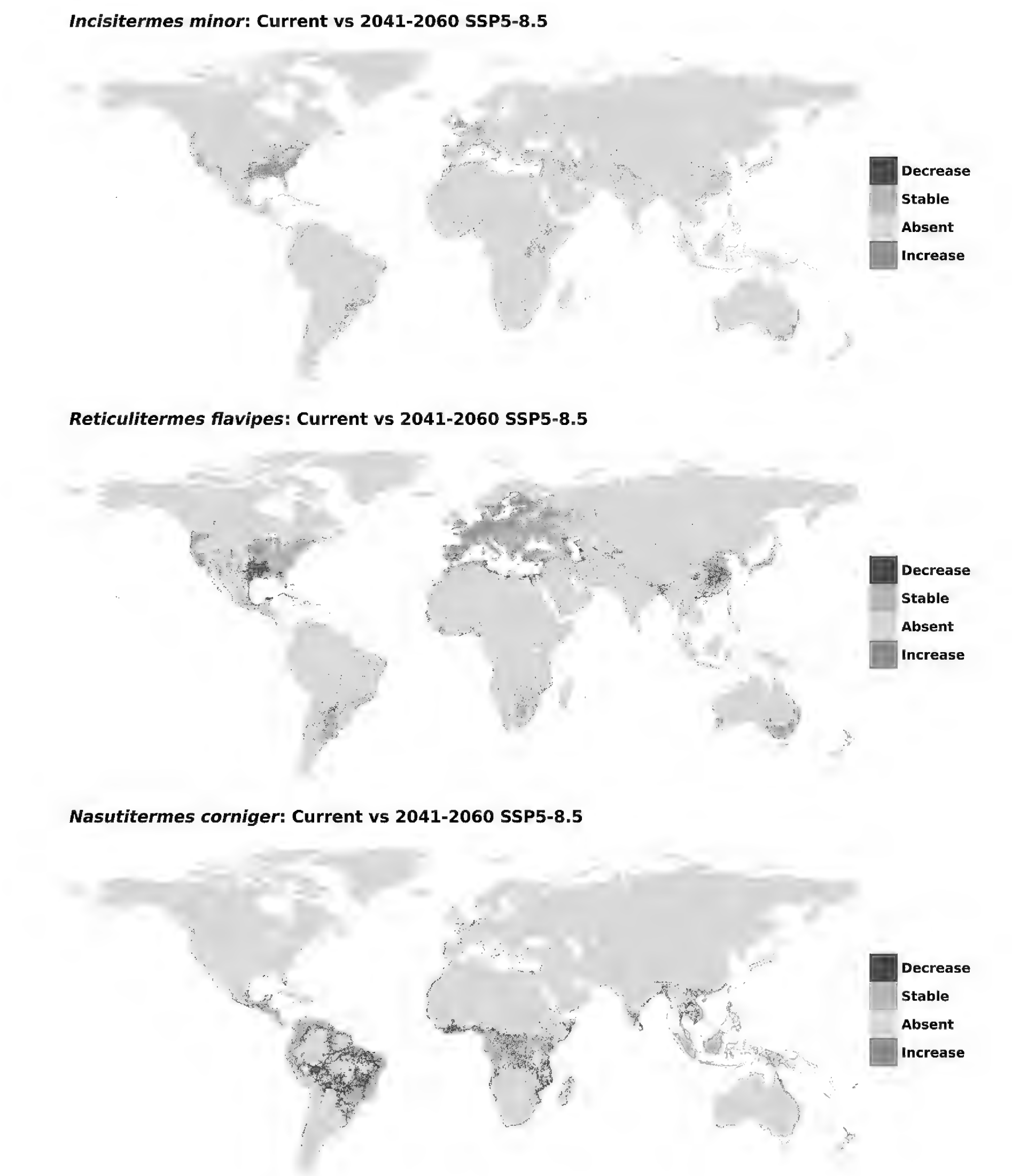
Figure 3. Potential projected range shift for *Incisitermes minor*, *Reticulitermes flavipes* and *Nasutitermes corniger* between potential current suitability and the period of 2041–2060 under the SSP5-8.5 scenario.

furniture to eastern US, Canada, China, various islands in the Pacific Ocean and Japan. In a pessimistic scenario (SSP5-8.5 2041–2060), *I. minor* is expected to extend its range across the US, Europe, Japan, China and Australia, particularly in densely urbanised regions (Fig. 3, Table 3). In contrast, according to our models, both *R. flavipes* and *N. corniger* show a lower dependency on urban environments,

especially *N. corniger*. *R. flavipes* is native to eastern US and northern Bahamas and has been introduced to Canada, Europe, South America and Easter Island. Under similar scenarios, its range potentially expands significantly across the US, Europe, southern Australia, southern Africa and southern South America. However, at the same time, its suitable range could decrease in southern US and in southern parts of China (Fig. 3, Table 3). On the other hand, *N. corniger*, originating from Neo-tropical Regions (Central and South America, West Indies), has established itself in only a few areas, in Florida and New Guinea. According to our models, *N. corniger* is projected to experience significant declines in its potential suitable tropical range, particularly in Africa and Brazil (Fig. 3, Table 3).

Discussion

The aim of our study was to predict the potential global spread of highly invasive termite species. We expanded the analysis beyond commonly considered bioclimatic and land-cover variables by incorporating elevation and connectivity factors, which encompass trade, transport and demographic patterns. Our objective was to forecast the short-term (2021–2040) and long-term (2041–2060) distribution of these species, considering climate change and socioeconomic development worldwide, under two shared socioeconomic pathways, SSP2-4.5 ("middle of the road") and SSP5-8.5 ("fossil-fuelled development"). Climate change, trade, transport and socioeconomic changes will be the main drivers of biological invasions in the coming decades (Essl et al. 2020). Despite their economic and ecological impact, only a few invasive termite species have been subject to distribution modelling so far (e.g. Li et al. (2013); Guerreiro et al. (2014); Tonini et al. (2014); Buczkowski and Bertelsmeier (2017); Goodman et al. (2022)).

Temperature and precipitation play a crucial role in determining the distribution of termites (Eggleton 2000), thereby explaining the predominant reliance on bioclimatic variables in most termite distribution models (Tonini et al. 2014; Buczkowski and Bertelsmeier 2017; Goodman et al. 2022). However, our study highlighted the importance of considering trade, transport and demographic factors in understanding termite invasions, with a particular emphasis on urbanisation and connectivity. Indeed, the period since the 1960s has witnessed an unprecedented upsurge in global transportation and urban expansion, catalysed by the advent of commercial jet aircraft. This trend highlights the escalating interconnectivity amongst urban hubs globally and its profound implications for termite population dispersal. The impact of propagule pressure on the success of invasions (Lockwood et al. 2005) further accentuates the critical significance of these aforementioned factors.

Our findings reveal that numerous invasive termite species could find suitable habitats in heavily urbanised and connected areas within major economic regions of every continent (excluding Antarctica). This trend is particularly evident as climate change and socioeconomic development intensify, providing more favourable bioclimatic conditions and human infrastructure for many species. Moreover, land-use changes – whether driven by urbanisation or deforestation for agriculture – profoundly shape species distribution (Jung et al. 2019). Our study introduces the use of land-cover variables within various scenarios of socioeconomic development, thereby enhancing the precision and accuracy of our climate and socioeconomic change projections. Our results align with other research studying climate change's impact on termites, showing an expansion of the distribution for several

economically important termite species worldwide (Buczkowski and Bertelsmeier 2017) and in South Korea (Lee et al. 2021). However, our study is more comprehensive, as it encompasses not only bioclimatic and/or elevation variables, but also land-cover and connectivity factors.

Variables' importance

Our study validates the significance of bioclimatic conditions as fundamental variables to understand termite distribution patterns (Eggleton 2000); amongst these factors, temperature emerges as the most influential determinant. We also note the minor influence of precipitation variables compared to temperature; a finding consistent with Guerreiro et al. (2014). It is worth noting, however, that invasive termites tend to establish nests within controlled-temperature human structures (Su and Scheffrahn 1998), highlighting the importance of considering not only bioclimatic factors, but also variables reflecting termite movements through these human structures ("connectivity" in this study). Our analysis highlights the significant role of the connectivity variables, particularly urban cover and Accessibility to Cities (ATC) and, to some extent, leisure vessels (LVE), in explaining the distribution of invasive termites. This echoes previous research showing the substantial predictive power of socioeconomic variables, ranking second only to bioclimatic and habitat variables (Bellard et al. 2016). The significance of human activity in facilitating the establishment of invasive termite populations is notable, given their primary reliance on wood, a ubiquitous commodity found in every household, boat and city worldwide. Regions with higher human activity should be predisposed to facilitating establishment of invasive termite populations. However, our results suggest that the human population (POP) layer contributes relatively little to the predictive capacity of our distribution models. This could be attributed to its high correlation with urban cover (0.53), suggesting potential redundancy with greater efficiency. Notably, areas such as seaports, airports and industrial zones, despite exhibiting lower population densities, exert a more pronounced influence on invasion risk compared to population density itself (Bellard et al. 2016).

Elevation (ELE) was found to play a minor role in predicting the distribution of invasive termites. While Guerreiro et al. (2014) reported a significant contribution of elevation to their model for *Cr. brevis*, our modelling revealed that the distribution of this species is primarily shaped by a combination of bioclimatic (bio11) and connectivity (urban and ATC) factors, with elevation contributing by less than 2%. If Guerreiro et al. (2014) used four variables (three bioclimatic factors and elevation) per species, our approach, utilising a comprehensive set of eight variables per species, likely attributed greater significance to other variables, reducing the prominence of elevation.

A previous study had integrated land-cover variables to project the spatial distribution of two invasive termite species (Tonini et al. 2014), but the extent of their contribution to the models was not reported. Here, excluding urban cover, the impact of land-cover variables – encompassing the cultivation of crops, including C3 perennial and C4 annual varieties, as well as forested, deforested and pasture areas – showed limited influence on the models. These results are expected given that agricultural crops are subject to significant disruption from human activities (e.g. pesticide applications). However, forthcoming environmental regulations and enhanced human health measures could bolster the survival rates of invasive termite species within these ecosystems (Haifig et al. 2008).

Current habitat suitability

Most of the ten invasive termites we studied show the ability to occupy a wide range of habitats, especially urban areas, confirming the global threat posed by invasive termites. Contrary to previous descriptions (Buczkowski and Bertelsmeier 2017), our models portray a more confined distribution, but with a heightened focus on urban and well-connected areas. This result is in line with the biology of invasive termites, often establishing themselves initially in urbanised localities before spreading to natural environments.

We also noted important differences for *Cr. brevis*, with a narrower suitable range compared to previous reports (Guerreiro et al. 2014; Buczkowski and Bertelsmeier 2017). This species primary inhabits in buildings outside its endemic range (Scheffrahn et al. 2009) and places of similar endemic climate such as Morocco (Najjari et al. 2023). Our modelling accentuated a preference for cities and economically developed regions, especially in the Americas and Africa. Interestingly, Asia and Europe, aside from major cities like Tokyo, Jakarta, Manila, Shanghai and the Guangdong-Hong Kong-Macao Greater Bay Area, showed less suitability, likely due to the presence of other *Cryptotermes* species in the Asia Pacific habitat (Scheffrahn et al. 2009; Guerreiro et al. 2014). Similarly, our models for *Cr. domesticus*, *Cr. dudleyi*, *Cr. havilandi* and *I. immigrans* identified limited distribution along the coastlines of tropical countries in Africa and South America, as well as suitability in most of Southeast Asia, especially Indonesia. The suitability is particularly high in major cities of these regions like São Paulo, Rio de Janeiro, Jakarta, Greater Bay Area or Lagos. This contrasts with the broader suitability suggested by Buczkowski and Bertelsmeier (2017) for these four species across tropical regions. These variations might be attributed to our comprehensive integration of land-cover, elevation and connectivity variables: elevation was a significant variable for *Cr. domesticus*, while C4 perennial crops was for *Cr. dudleyi*, leisure vessels (LVE) for *Cr. havilandi*, and both Accessibility to cities and urban land for *I. immigrans*. A similar divergence emerged for *I. minor* in higher latitudes, highlighting the strong influence of large urbanised and connected areas (e.g. most large US cities, southern California, São Paulo, London, Belgium, Madrid, Greater Bay Area and main cities of eastern Australia).

Our models for *Co. formosanus* and *Co. gestroi* also showed a distribution heavily associated with urban areas (see also Li et al. (2013) and Tonini et al. (2014)) both in their native and introduced regions. The use of connectivity variables for both species likely contribute to these results, accounting for 50% and 44% to the models, respectively. On the other hand, we identified suitability for *Co. gestroi* in European and American cities, such as Paris, London, Madrid or New York, although such suitability is highly improbable due to the species' restriction to tropical regions, necessitating favourable conditions, such as adequate humidity and high temperatures (Li et al. 2013). Nonetheless, our models indicate high suitability for *Co. gestroi* in more likely regions, such as large economic areas in tropical and subtropical regions like western Africa, Southeast Asia or south-eastern China. Conversely, *Coptotermes formosanus*, with a warm temperate to subtropical distribution (Cao and Su 2016), presented heightened risk in large cities of south-eastern US and Asia, as well as South America. As the effects of climate change reshape ecosystems globally, disparities between the two species are likely to become more apparent, especially considering instances like *Co. formosanus*

potentially expanding its range into the Korean Peninsula due to increasing temperatures (Lee et al. 2021).

Regarding *Reticulitermes flavipes*, our models suggest a threat to most cities in temperate and subtropical regions, particularly in its native range in the US, but also in Europe and eastern Asia, with a notable focus on urban areas (the urban layers contribute 36% to the projections). Our results partially disagree with those of Buczkowski and Bertelsmeier (2017) who suggested potential suitability in higher latitudes (e.g. Iceland, Norway, Alaska or Patagonia) and the Tropics (Indonesia, Ecuador, Colombia). Such locations appear unlikely given the current distribution of the species (Evans et al. 2013). Modelling also shows that the distribution of *R. flavipes* does not extend to cold regions, such as the Alps or the Carpathians in Europe, a limitation attributed to the elevation layer.

Finally, our results suggest that *N. corniger* is highly adapted to tropical regions. Our results agree with those of Buczkowski and Bertelsmeier (2017), except that the latter also designate parts of southern Argentina, Chile, Morocco, the Arabian Peninsula and Australia as potentially suitable. This seems unlikely, as this species is strictly restricted to tropical regions, its actual distribution ranging from southern Mexico to southern Brazil and northern Argentina, including most of the West Indies (Scheffrahn et al. 2005).

Key functional traits to invasive success

Facon et al. (2006) proposed three scenarios to understand the relationship between invasive species and their new environments, shedding light on the role of human activities in biological invasions. The first scenario suggests that invasion is limited by the small population size of the invasive propagule (to establish a viable population), but changes in migration patterns, possibly caused by human activity, can trigger the invasion. The second scenario suggests that invasion can proceed if the introduced species finds a suitable match with the environment; this adequacy can be facilitated by changes in the biotic or abiotic environment, changes often influenced by human activities. The third scenario highlights genetic changes in the invader as a factor initiating invasions, including reduced genetic variance, inappropriate range of adaptive variation in the original species and maladaptation due to excessive migration. Invasive termites fit perfectly within this framework. Migration change (e.g. by wood exchanges through furniture or private vessels) and human activities in urban areas offer many opportunities to establish and invade new territories. Evans et al. (2013) identified three characteristics common to all 28 invasive termite species that increase their likelihood of successful propagule. First, invasive termites are all wood feeders (Table 1).

Secondly, nesting in wood is particularly advantageous for invasions given the ubiquitous presence of wood in households worldwide (e.g. Grace et al. 2009). While some species live, eat and nest exclusively in wood (called single-piece nester, here the Kalotermitidae species), others (here the Rhinotermitidae species) begin their colonies within wood or at the soil-wood interface before establishing their colonies underground or in another piece of wood (Ferraz and Cancello 2004; de Lima et al. 2006). The latter are called intermediate-piece nesters and will forage outside their colony after this single-piece stage (Abe 1987). *Nasutitermes corniger*, though typically nesting on trees, poles, walls or directly on the ground (Thorne 1980), can also establish an incipient colony inside small wood pieces (Thorne and

Haverty 2000; Scheffrahn et al. 2014). All ten invasive species can, therefore, use wood as a hidden mean of transport for at least part of their lifecycle.

All ten invasive species share a third characteristic: the ability to produce secondary reproductives, typically through neoteny of nymphs (nymphoid reproductives), workers or pseudergates (ergatoid reproductive) or through the retention of alates (adultoid reproductive) (Myles 1999). In the case of *N. corniger*, ergatoids are produced, rendering any piece of wood with foraging workers a viable propagule at any time of year (Thorne and Noirot 1982). These ergatoids, combined with the fact that they are polygynous, probably allowed *N. corniger* to invade New Guinea 100 years ago via sugar trade shipping from the West Indies, travelling more than 15,000 km (Roisin and Pasteels 1986; Scheffrahn 2013).

Consequently, all ten of our highly-invasive species are capable of nesting in wood, whether in furniture or in boats (Scheffrahn 2023; Chouvenc, personal communication, January 2024), rendering invasions extremely likely, be it from one household to another or from a marina to nearby coastal residences, as exemplified by *N. corniger* or *Coptotermes* (Scheffrahn and Crowe 2011; Scheffrahn et al. 2014; Hochmair et al. 2023; Scheffrahn 2023). Flying imagoes are attracted by light poles and illuminated houses near marinas, serving as an initial entry point into the lands (Scheffrahn et al. 2014; Scheffrahn, personal communication, January 2024). However, once arriving in a new environment, invasive species may face new challenges in establishing themselves if the environment differs or is already saturated by other species. To succeed under such conditions, the species may undergo substantial adaptations (Facon et al. 2006). For example, native populations of *Reticulitermes flavipes* consist of colonies headed by monogamous pairs of primary reproductives; in contrast, introduced populations in France exhibit a breeding structure where hundreds of related neotenics reproduce while colonies lose intraspecific aggression and get a propensity to fuse (Perdereau et al. 2013; Perdereau et al. 2015). These changes in colonies composition and organisation confer advantages in terms of resource exploitation and competition, thus facilitating ecological dominance.

Some termite species have biological and/or behavioural characteristics that can help them invade and survive in new territories. For instance, *Reticulitermes* species are naturally well-adapted to low temperatures and can move the nest to deep underground during the winter (Cabrera and Kamble 2001; Takata et al. 2023). This behavioural trait can prove decisive in extending their range northwards (Cabrera and Kamble 2001; Takata et al. 2023). Additionally, climate change may relax constraints on naturalisation and, hence, increase the hybridisation risk amongst invasive and native populations (e.g, *Co. gestroi* and *Co. formosanus* in Florida), further influencing invasion dynamics (Chouvenc et al. 2015; Fournier and Aron 2021). Elevated temperatures also enhance termite foraging activity (Kasseney et al. 2011; Zanne et al. 2022). For example, *Co. gestroi* and *Co. formosanus* have a significantly higher wood consumption rate between 22–35 °C than between 10–15 °C (Patel et al. 2019). Finally, biological invasions could also be facilitated by the bridgehead effect (Lombaert et al. 2010). Introduced populations are often the source of other invasions (Yang et al. 2012; Sherpa et al. 2019; Blumenfeld and Vargo 2020). These secondary invasions, therefore, originate from populations that have already succeeded in overcoming all the barriers – geography, survival, reproduction, dispersal, environment – that punctuate from introduction to propagation invasion processes. For instance, native to eastern Asia, *Co. formosanus* first established populations in Hawaii before invading the US mainland (Blumenfeld et al. 2021).

What to expect in the future: combined effects of global warming, urbanisation and growing connectivity

Urbanisation is an inevitable phenomenon as projected by the United Nations Department of Economic and Social Affairs (UN DESA 2020): up to two-thirds of the global population is expected to reside in urban areas by 2050. Moreover, the number of megacities (with over 10 million inhabitants) is projected to rise from 33 in 2018 to potentially 43 in 2030. Urbanisation and megacities, notably through the urban heat-island effect (Szulkin et al. 2020), will therefore constitute invasion hotspots that may serve as bridgeheads in surrounding natural habitats as temperatures increase due to climate change. Our study demonstrates that most species could thrive in a changing climate and an increasingly urbanised world, particularly under a fossil-fuelled future (SSP5-8.5). This finding aligns with other studies on different and shared species and using different variables, collectively suggesting a consensus that climate change will generally increase the distribution of most invasive or pest termites (e.g. Tonini et al. (2014); Buczkowski and Bertelsmeier (2017); Lee et al. (2021)). While some species might experience localised contractions in their ranges, they are anticipated to make gains in other regions, particularly within densely urbanised areas. This trend is evidenced by our incorporation of connectivity variables, which reveals the potential for more substantial and costly damage. For instance, our modelling shows that *Cr. brevis* could experience a reduced tropical range, yet extend its distribution into urbanised higher latitude regions. Thus, a contraction in range does not necessarily translate into a reduction in damage costs, especially for termites that predominantly target human structures, such as species from the Kalotermitidae and Rhinotermitidae families. Conversely, other species like *Co. formosanus* could mainly expand their range, with close to zero reduction compared to their potential current suitable habitat. The Formosan subterranean termite could potentially thrive in higher latitudes in a fossil-fuelled world, placing most American, European and eastern Asian cities at risk. On the other hand, *N. corniger* will lose significant suitability in a fossil-fuelled world within Brazil and central Africa, probably due to the combined effects of increased deforestation and less favourable bioclimatic conditions.

Overall, most of these ten invasive termites will thrive in a changing climate and a heavily transformed world marked by escalating urbanisation, particularly under a fossil-fuel-dependent trajectory. Even if our models do not consider the full force and speed of future connectivity, the undeniable expansion potential of the ten termite species and, therefore, the damage concomitant with invasions, underscores the urgency of addressing climate change, urbanisation and growing connectivity. These factors will be crucial in contributing to the spread of invasive termites, posing a significant threat not only to the economies of invaded regions, but also, to some extent, to biodiversity and ecosystem functioning.

Conclusion

As our world becomes increasingly interconnected and urbanised, it is imperative to recognise the importance of incorporating connectivity variables – trade, transport and demography – into invasive species distribution modelling, particularly for termites. We have demonstrated that ten highly-invasive termite species could

potentially spread to heavily-urbanised and connected areas in tropical, subtropical and, to a lesser extent, temperate regions. This risk is amplified with the combined effects of global warming, urbanisation and growing connectivity. Most species could experience expanded ranges or find suitable habitats in more urbanised and connected areas, resulting in costly damage regardless of range shifts. Major cities, particularly in tropical, subtropical and temperate areas, should swiftly implement rigorous termite control measures and citizen-science initiatives to prevent and detect further invasions before irreversible damage occurs.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Edouard Duquesne: Data curation, Formal analysis, Methodology, Software, Visualisation, Writing – original draft.
Denis Fournier: Conceptualisation, Funding acquisition, Supervision, Visualisation, Writing – original draft, Writing – review & editing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary tables and figures (S1 to S7)

Authors: Edouard Duquesne, Denis Fournier

Data type: docx

Link: https://doi.org/10.3897/neobiota.92.115411.suppl1

Supplementary material 2

Occurrences of the 22 invasive termites as well as their source

Authors: Edouard Duquesne, Denis Fournier

Data type: xlsx

Link: https://doi.org/10.3897/neobiota.92.115411.suppl2